

Circadian rhythms of sexual behavior and pheromone titers of *Holcocerus arenicola* (Lepidoptera: Cossidae)

JING Xiao-Yuan¹, ZHANG Jin-Tong^{1,*}, LUO You-Qing², LIU Pei-Hua³,
ZONG Shi-Xiang², LIU Jin-Long¹, YANG Mei-Hong¹

(1. Institute of Chemical Ecology, Shanxi Agricultural University, Taigu, Shanxi 030801, China;

2. School of Resources and Environment, Beijing Forestry University, Beijing 100083, China;

3. Forestry Station of Yuyang District, Yulin, Shaanxi 719000, China)

Abstract: The calling and mating behavior of *Holcocerus arenicola*, a primary root-boring pest of sand *Salix* (*Salix psammophila*) were observed during the 6 h of the scotophase to investigate their activity rhythm. The pheromone titer was analyzed by the electroantennogram (EAG) and gas chromatograph (GC) to determine the diel periodicity of pheromone production during one scotophase and the effect of female age on pheromone production. The results showed that most females initiated calling during the 0.5–1 h after lights off, and the maximum calling occurred during the 2nd night after emergence. The mating was observed during the 1–2 h of the dark phase, and the mating percentage of 1-d-old females was the highest. Mating lasted for an average of 24.16 ± 2.64 min and occurred earlier as females got older. The sexual activity of 5- to 6-d-old females was rarely observed in the test. The synthesis of pheromone started 1–2 h prior to the onset of calling and reached a peak during the first 2 h of the scotophase. The pheromone titer during the calling period decreased significantly with age, being highest in extracts from newly emerged females. Field trial showed that traps baited either with virgin females or female sex gland extracts could effectively capture males. These results suggest that there was a synchronous relationship between the pheromone titer and the sexual activity, and also a potential use of long-range sex pheromone for the control of *H. arenicola*.

Key words: *Holcocerus arenicola*; *Salix psammophila*; sexual activity; sex pheromone; diel periodicity

1 INTRODUCTION

The sand *Salix* carpenterworm, *Holcocerus arenicola* Staudinger (Lepidoptera: Cossidae), one of the serious root-boring forest pests in desert areas, is widely distributed in Shaanxi, Inner Mongolia, Gansu, Xinjiang and Ningxia provinces in China, and Russia, Mongolia, Asia minor and Caucasia. A generation of *H. arenicola* may last four years, and mature larvae transfer to the sand-soil from the host roots and begin to pupate under the ground in May every year. The primary host of *H. arenicola* is sand *salix*, besides other alternative hosts including *Heey aprum*, *Hippophae*, *Salix microstachya*, *Caragana korskinskii*, etc. (Hu et al., 1987).

Sand *Salix*, *Salix psammophila* (Salicaceae), one kind of shrub or sub-arbor tree, is mainly used

to control desertification, to conserve land and water resources, and to provide fodder and shelter for wild and domestic animals in the northwestern desert areas in China. The larvae of *H. arenicola* have the habit of aggregating in dozens or hundreds to burrow and hollow the stems and roots, which directly cause sand *Salix* forests to wither to death. In Qinghai Province, for example, infestation levels of sand *Salix* by *H. arenicola* reached 35% (Xie, 2008). The damage is so severe and extensive that the sand *Salix* carpenterworm is considered as a major threat to the continued existence of sand *Salix* forests in China.

It is very difficult to control *H. arenicola* with traditional insecticides because of the wood boring habits of the larvae in the rhizome. Nevertheless, sex pheromones produced by target species were particularly appealing for insects of the family

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Brief introduction of the first author: JING Xiao-Yuan, born in 1969, PhD student, majoring in chemical ecology, E-mail: jingxiaoyuan@126.com

* Corresponding author, E-mail: zhangjintong@126.com

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Cossidae that develop in protected places and thus were not easy to be controlled with insecticides (Zhang *et al.*, 2001, 2009; Fang *et al.*, 2005; Chen *et al.*, 2006). Thus far, any research on the sex pheromone of *H. arenicola* has not been reported, except for biological characteristics of this insect. In this paper, we report the results of the effect of age and time on sexual activity and pheromone production of *H. arenicola*.

2 MATERIALS AND METHODS

2.1 Experimental insects

H. arenicola pupae were collected from sand-soil (1 m in diameter, 15 cm in depth) around the sand Salix damaged badly by the sand Salix carpenterworm in the Balasu woodland, Yulin, Shaanxi, China, in mid-May 2008. Then, 100–150 collected pupae were buried in sands (containing 5%–8% water) 15 cm in depth in a wooden box (40 cm × 60 cm × 30 cm) covered with nylon mesh. In total, 12 boxes were prepared. These boxes were maintained in our lab at 26–30°C, 70%–80% relative humidity, and a natural photoperiod (14L:10D, lights went on at 6:00 and off at 20:00).

2.2 Investigation of calling and mating

After emergence, the adults were segregated by sex and transferred into cages (80 cm × 80 cm × 80 cm) containing a source of 8% sucrose solution with 50 individuals per cage. Males and virgin females were kept in different cages, which were placed with a distance of 20 cm. Adults emerging between 0 and 24 h were considered as 1-d-old. The calling behaviors of adult moths were investigated every 30 min during the 6 h of the scotophase because preliminary tests showed that sexual activity only occurred during this period. The mean value of the two recordings per hour was taken to calculate the proportion of calling females according to the criteria for calling behavior (Zhang and Meng, 2001). A single red incandescent light bulb controlled by a rheostat was used to illuminate for observing with a light intensity of approximately 0.5 lux during the scotophase. Three replicates with 150 females in total were investigated.

Mating behavior was studied by the following method: Three cages with 20 pairs of newly emerged adults (<10 h old) per cage were set up and mating behaviors were observed at 30-min intervals during the 6 h of the scotophase on 6 different nights. Mating pairs were gently transferred into a small cage

(30 cm × 30 cm × 30 cm) for the measurement of mating duration. The numbers of pairs starting to copulate at different time of the scotophase were calculated and were transformed into percentages. Three replicates with 60 pairs of adults in total were observed.

2.3 Extracts of the sex pheromone

When the females began calling, sex pheromone glands were extruded immediately by applying gentle pressure to the female's abdominal tips to force eversion of the ovipositor, and were excised with small scissors and put into a 2-mL glass vial containing 500 µL of distilled n-hexane in which 1-undecanol was added as the internal standards (Zhang *et al.*, 2001). Glands were extracted for 20–30 min, and then the solvent were transferred to a clean vial. Extracts were stored at –20°C if not used immediately. Extracts which contained 5 FE (female equivalent), were concentrated to 1 µL under a gentle stream of N₂ before analysis (Rojas *et al.*, 2006).

2.4 Analysis of pheromone titer

Two experiments, using an electrophysiological assay, were carried out to examine the diel periodicity of pheromone production during one scotophase and the effect of female age on pheromone production. In both experiments, extracts were obtained as above and the responses of male antennae to 5 FE extracts were determined using an electroantennographic detection apparatus, EAD (Syntech, Hilversum, the Netherlands). An antenna from a 1-d-old male was excised at its base, and the distal part of the terminal segment was cut off. The antenna was suspended between glass capillary electrodes filled with insect physiological saline (7.5 g NaCl, 0.21 g CaCl₂, 0.35 g KCl, 0.20 g NaHCO₃ per liter distilled water) (Beadle and Ephrussi, 1936; Zhang and Meng, 2000).

In the first experiment, we tested female gland extracts taken from 1 to 6-d-old virgin females at the onset of calling to determine the effect of female age on pheromone production. Three replicates with a total of 90 females were performed. In the second experiment, extracts were taken at hourly intervals from 1-d-old females during –1–4 h of the scotophase to determine the diel periodicity of pheromone production by virgin females. The male antenna was hourly replaced by fresh one and 90 glands were determined.

Meanwhile, quantitative analyses were conducted on a coupled gas chromatography and electroantennographic detection (GC-EAD) consisted of EAD described previously and a HP 6890 gas

chromatograph (GC) equipped with a flame ionization detector (FID) and a splitless injector. A nonpolar column (HP-5, 5% phenyl methyl siloxane 30 m $\times$ 0.32 mm i. d. $\times$ 0.33 μ m film thickness, Palo Alto, CA., USA) was used with a temperature program of 80°C for 2 min, 4°C/min to 180°C, then 10°C/min to 240°C, isothermal for 15 min. Injector and detector were set at 250°C. Pure nitrogen was used as the carrier gas at a linear flow rate of 46 cm/s. At the end of the capillary column, a splitter distributed the effluent from the column to the FID and to a transfer line toward the EAD. Both connection tubes were made of deactivated silica of the same length and diameter, so that the column effluent was split ($\approx 1:1$) (Rojas *et al.*, 2006). The integrated areas of selected peaks were compared to the corresponding data of internal standards. Changes in pheromone titer at different moth ages were determined at the onset of calling. Changes in pheromone titer at different time of the scotophase were determined with glands of 1-d-old (age with the maximal mating) females.

2.5 Attraction of males in the field

A short field trial was run for three days in a sand Salix forest at Yulin, Shaanxi, China, from 15–20 June 2008. Delta sticky traps were baited with two virgin females, two virgin males (virgin moths in small mesh cages suspended in traps), a lure treated with 0.5 mL of a 10 FE pheromone gland extracts or a lure treated with 0.5 mL of hexane as a control. There were 9 replicates of each treatment, with traps spaced 20 m apart and hung from branches 1 m above the ground. Capture data were transformed to $\log(x + 1)$ before the differences between means were tested for significance by analysis of variance.

2.6 Data analysis

Statistical analysis was performed using the SPSS 10.0 statistical package (SPSS Inc., Chicago IL). The data obtained were submitted to one-way analysis of variance (ANOVA) by the *F* test, and the means were compared by Tukey's test. Arcsine transformations were performed where appropriate on data involving percentages or proportions before the use of analysis of variance.

3 RESULTS

3.1 The rhythm of calling and mating

The pattern of *H. arenicola* calling females at different ages during the scotophase is shown in Fig. 1. Calling activity was initiated during the 0.5–1 h after lights off and terminated during 4–5 h of the

scotophase. Most females initiated calling at night they emerged (although a small proportion did so at subsequent nights), and constant calling activity was observed on the following nights (Fig. 2). Maximum calling occurred during the 2nd night after emergence (88.3%). The percent calling of 2 to 5-d-old females during the first 2 h of the scotophase was significantly higher than that of 1-d-old females (Fig. 1), which is probably the reason that more females reached sexual maturity and were ready to mate on subsequent nights than on the first night. In addition, the male moths were extraordinarily active and excited, exhibiting frequent flight and collision into the walls of the screen cage during the calling period. Some female moths finished eclosion in the daytime, but none of them started calling until nightfall.

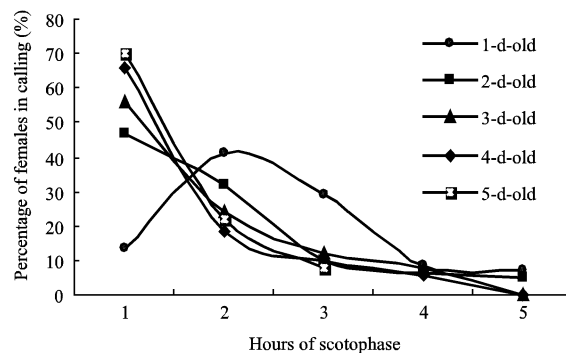


Fig. 1 Effect of age and time in scotophase on calling by *Holcocerus arenicola* females

Observations at 30-min intervals ($N=3$; 150 females were investigated).

Values represent the mean percentage of 2 recordings per hour.

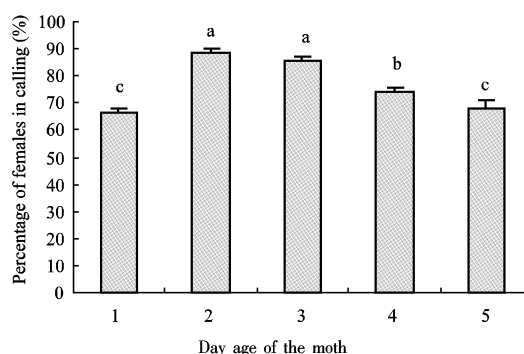


Fig. 2 The percentage (mean $\pm$ SD) of *Holcocerus arenicola* calling females of different ages ($df=4, 10$; $F=80.118$; $P < 0.001$)

Bars with different letters are significantly different ($N=3$, subset for $\alpha=0.05$).

The mating behavior of adult moths mostly happened on the upper walls or beneath the top of the screen cage. The maximum mating of 1-d-old

moths occurred during the 2nd hour of the scotophase, while the maximum mating of 2 to 4-d-old moths were observed during the 1st hour after lights off (Fig. 3). Statistical results of the adult mating showed that the mating percentage of different-aged virgin females varied significantly. The highest mating percentage was found in 1-d-old females, reaching 54%, followed by 2-d-old (28.5%), 3-d-old (12%), and 4-d-old (5.5%). The mating behavior of 5- to 6-d-old moths was rarely observed. Mating lasted for an average of 24.16 ± 2.64 min (mean $\pm$ SD, $df = 5, 12$; $F = 0.808$; $P < 0.001$), ranging from 20–32 min.

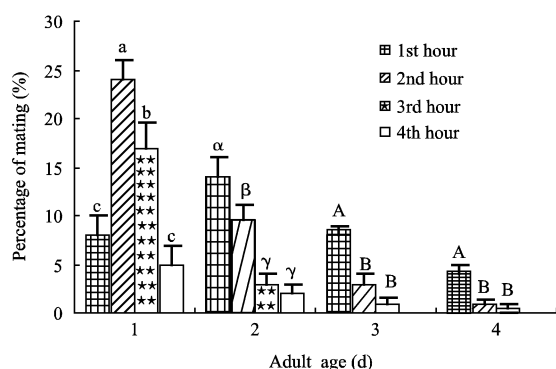


Fig. 3 The percentage (mean $\pm$ SD) of mating behavior of *Holcocerus arenicola* in different ages and time
For 1-d-old moths: $df=3, 8$; $F=47.368$; $P < 0.001$;
for 2-d-old moths: $df=3, 8$; $F=46.560$; $P < 0.001$; for 3-d-old moths: $df=2, 6$; $F=46.429$; $P < 0.001$; for 4-d-old moths: $df=2, 6$; $F=27.003$; $P < 0.001$). Bars with different letters are significantly different ($N=3$, subset for $\alpha=0.05$).

3.2 The rhythm of sex pheromone titer

The EAG responses of 1-d-old male antenna clearly showed that the titer of pheromone present in the gland at the time of calling varied significantly, being highest in extracts from newly emerged females (Fig. 4). There was a significant decrease in the titer of pheromone with age, explaining the lower mating percentage of 3 to 4-d-old females relative to 1 to 2-d-old females.

There was also evidence of diel periodicity in pheromone production (Fig. 5). The highest EAG response of male antenna was observed with extracts from taken at 21:00, an hour after lights off, and coincided with the time of peak mating (Fig. 3). However, the extracts prepared at 19:00, an hour before lights off, could elicit a distinct EAG response, indicating that sex pheromone had been produced before the calling gate opening.

GC-EAD analysis of female gland extracts showed that the peak B with the maximum content could elicit

the strongest EAG response (Fig. 6). Peak B was identified as a major component of the sex pheromone of *H. arenicola* by gas chromatography-mass spectrometry (GC-MS), micro-analytical reaction and field trapping trials (unpublished), and its amount could be calculated by reference to the integral areas of internal standards.

Quantitative analysis by GC of the effect of female age on pheromone production showed that the amount of the major component (peak B) in extracts from 1-d-old females was the highest (5.63 ± 0.30 ng), followed by that from 2-d-old (3.87 ± 0.42 ng), 3-d-old (2.23 ± 0.09 ng), 4-d-old (1.83 ± 0.06 ng), 5-d-old (0.87 ± 0.14 ng) and 6-d-old (0.78 ± 0.26 ng) females respectively in a single female sex gland. Based on the comparison of Fig. 3 and Fig. 4, the results of GC, EAG and mating investigation are consistent in explaining the variation of sexual activity with age.

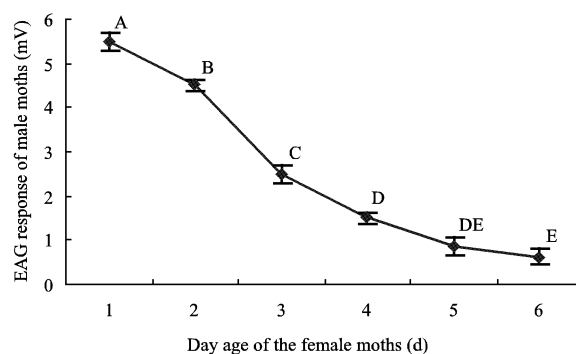


Fig. 4 The EAG response (mean $\pm$ SD) of male moths to the sex gland extracts of different aged female moths at calling time ($df=5, 12$; $F=322.24$; $P < 0.001$)

Bars with different upper-case letters above are highly significantly different ($N=3$, subset for $\alpha=0.01$).

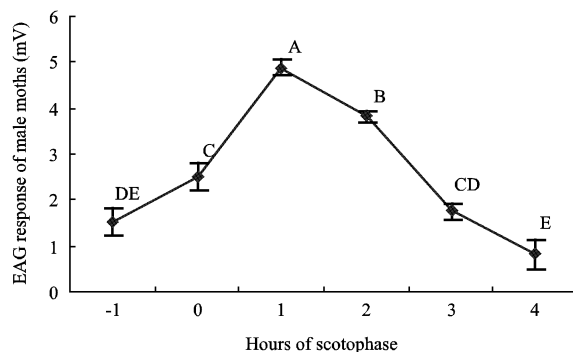


Fig. 5 The EAG response (mean $\pm$ SD) of male moths to the sex gland extracts of female moth at different time in dark cycle ($df=5, 12$; $F=117.52$; $P < 0.001$)

Bars with different upper-case letters above are highly significantly different ($N=3$, subset for $\alpha=0.01$).

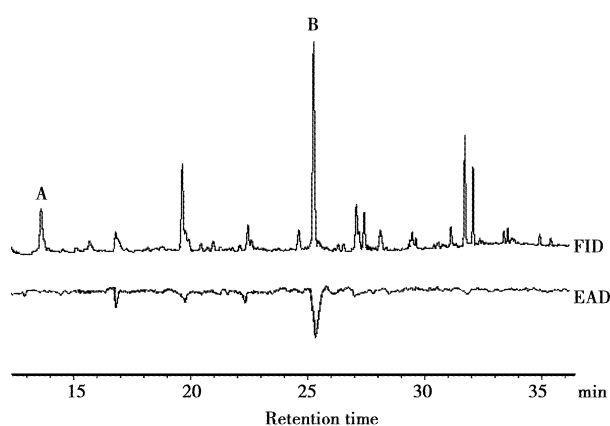


Fig. 6 The GC-EAD analysis of sex gland extracts of female moths
Peak A: The internal standards (1-undecanol); peak B: The major active component of the sex pheromone of female moths.

Likewise, the GC analysis for the diel periodicity of pheromone production during one scotophase showed that the titer of peak B was highest during the first 2 h of the scotophase and varied significantly throughout the calling period. The amount of peak B in extracts taken at different time was listed as follows: 1.97 ± 0.02 ng (–1 h), 2.93 ± 0.17 ng (0 h), 4.55 ± 0.12 ng (1 h), 3.39 ± 0.04 ng (2 h), 1.89 ± 0.13 ng (3 h) and 1.52 ± 0.24 ng (4 h). Together with the EAG analytical results (Fig. 5), it revealed that the production of the pheromone increased gradually with the time, up to a maximum at the 1st hour, and then began to decline until it fell to a minimum at the 4th hour of the dark cycle. The diel periodicity of sex pheromone production deduced from GC and EAD are in accordance with that of mating behavior of adult moths.

3.3 The field attraction of males

Traps baited with males or n-hexane (control) failed to attract male *H. arenicola* in the field. However, traps baited with virgin females or female extracts in a solvent (10 FE) caught on average 9 and 5 males per trap per day, respectively (Table 1). Males of *H. arenicola* were captured in traps baited either with virgin females or female extracts, suggesting the use of a long-range sex pheromone for control of this pest.

4 DISCUSSION

Age affected the sexual activity of *H. arenicola*. The calling and mating occurred earlier as females got older. Similar results have been reported for several other moths (Howlader and Gerber, 1986;

Table 1 The field attraction of male *Holcocerus arenicola*

Treatment	Mean trapped moths ($N=9$) (mean $\pm$ SD)
Males	0
n-hexane	0
Virgin females	9 ± 2.45 A
Female extracts	5 ± 1.58 B

Notes: Means ($df = 3, 32$; $F = 80.471$; $P < 0.001$) were compared by One-way ANOVA, and data followed by different letters are significantly different (subset for $\alpha = 0.01$).

Kou and Chow, 1987; Delisle and Royer, 1994; Edmonds *et al.*, 2000). It has been suggested that the advance in the onset of time of calling and mating with age in lepidopteran species is an adaptation that permits older females to increase their chances of attracting mates before younger females start calling (Delisle, 1995; Mazor and Dunkelblum, 2005).

There was a synchronous relationship between the amount of pheromone in the glands and the sexual activity at different ages. For *H. arenicola*, mating started on the 1st night, decreased on the 4th night, and mating behavior of 5- to 6-d-old moths was rarely observed. The decrease in pheromone titer paralleled with the mating activity. Although more calling was observed on the 2nd-3rd night from emergence (Fig. 2), one possible reason is that most females actually called but didn't mate on the 1st night and continued calling on subsequent night.

The relationship between sexual activity and pheromone titer during the scotophase also was synchronous. The sexual activity of *H. arenicola* was almost constant during the first half of the scotophase. However, there was more calling and mating during the first 2 h of the scotophase (Fig. 1 and Fig. 3), accompanied by an increase in pheromone titer (Fig. 5). Thereafter, the pheromone production titer and sexual activity decreased gradually and reached at the minimal level at the 4th hour of the scotophase. However, the extracts taken at 19:00 (an hour before lights off) when most female moths had never initiated calling or mating, could elicit a distinct EAG response. It revealed that the production and release of sex pheromone were not in synchronization and the synthesis of pheromone started some hours prior to the onset of calling. The content of pheromone increased progressively and reached a peak in the first or second hour of the scotophase, but declined once females expressed calling behavior.

During the investigation of calling behavior, it was found that the calling behavior was hardly

observed on rainy days or days of a lower temperature. Appel and Rust (1983) reported similarly that a lower temperature affected the production of and response to sex pheromone by the American cockroach. In addition, under windless conditions, the calling percentage was low, and the mating percentage also decreased along with it, while artificial wind provided with an electric fan could significantly increase the calling percentage. Besides temperature and wind velocity, the various abiotic and biotic factors, such as host plants, day length, light intensity and relative humidity could impact on pheromonal communication (McNeil, 1991).

The data obtained in this study clearly demonstrated that *H. arenicola* females produced a sex pheromone. Furthermore, the sex pheromone was not synthesized immediately in the sex glands after eclosion, but synthesized maximally during the 0.5–1 h after lights off when sex pheromone glands should be extracted for a series of studies. Furthermore, the field trapping trial demonstrated the existence of a long-range sex attraction and its potential use for control of *H. arenicola*.

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沙柳木蠹蛾性行为及其性信息素滴度的动态节律

荆小院¹, 张金桐^{1,*}, 骆有庆², 柳培华³, 宗世祥², 刘金龙¹, 杨美红¹

(1. 山西农业大学文理学院化学生态研究所, 山西太谷 030801; 2. 北京林业大学资源与环境学院, 北京 100083;

3. 陕西省榆林市榆阳区林业工作站, 陕西榆林 719000)

摘要: 沙柳木蠹蛾 *Holcocerus arenicola* 是为害沙柳 *Salix psammophila* 的主要钻蛀性害虫之一。在进入暗期后的 6 h 内, 对其求偶行为和交配行为进行观察和记录, 调查该虫求偶和交配的活动规律。通过触角电位技术(EAG)和毛细管气相色谱(GC)对性腺体内信息素的滴度进行了分析, 以揭示性信息素产生的昼夜节律和雌虫日龄对性信息素合成的影响。结果表明: 该虫在暗期 0.5~1 h 内即开始有求偶行为, 最大求偶高峰出现在羽化后的第 2 晚。交配行为主要发生在暗期的 1~2 h 内。在各日龄的成虫中, 1 日龄成虫的交配百分率最高。交配平均时间为 24.16 ± 2.64 min, 随着日龄的增加, 交配时间前移。在实验中, 未观察到 5~6 日龄成虫的交配行为。沙柳木蠹蛾性信息素的体内合成早于求偶行为 1~2 h, 并在暗期的前 2 h 内达到峰值。性信息素的滴度随着雌虫日龄的增减而减少, 最高值为当日羽化雌虫的腺体提取物。林间诱蛾实验中, 处女雌蛾和性腺体提取物对雄蛾均有较好的诱捕效果。本研究表明, 在沙柳木蠹蛾的性信息素滴度和性活动之间具有同步关系, 同时为进一步利用长距离性信息素防治该虫提供了参考。

关键词: 沙柳木蠹蛾; 沙柳; 性行为; 性信息素; 昼夜节律

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